

# Anticipatory postural adjustments stabilise the whole upper-limb prior to a gentle index finger tap

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**Abstract** Little is known about anticipatory postural adjustments (APAs) developing when body segments of tiny mass are moved. Thus, APAs in the human upper-limb were investigated during a gentle and small index finger tap (35 mm stroke in 50 ms). This task was fulfilled by ten subjects either with prone or supine hand. EMG was recorded from Flexor Digitorum Superficialis (FDS), the prime mover, and from several upper-limb muscles under slight tonic contraction. Regardless of hand posture, EMG was inhibited in Flexor Carpi Radialis and facilitated in Extensor Carpi Radialis well before the FDS burst. With the prone hand, the prime mover activity was preceded by Biceps inhibition and Triceps facilitation; this effect reverted in sign with the supine hand. A postural reversal was also observed in Anterior Deltoid and Trapezius which were both inhibited with the prone hand. The effect in Trapezius was present only with the unsupported forearm. It is thus demonstrated that a gentle small finger tap produces well-defined anticipatory natural synergies behaving as the most “classical” APAs: (1) they are distributed to several upper-limb muscles creating a postural chain aiming to prevent the effects of the interaction torques generated by the voluntary movement; (2) they change in amplitude according to the level of postural stability and (3) they revert in sign when movement direction is reverted. These results are also corroborated by data obtained from a simple mechanical model simulating finger tapping

in a fictive upper-limb. A possible role of APAs in controlling movements’ accuracy is also discussed.

**Keywords** Motor control · Posture · APAs · Interaction torques · Dysmetria · Human

## Introduction

As highlighted by Massion (1992), a movement is always accompanied by interaction torques, acting on both the supporting segments and the rest of the body, which change the *segmental* posture and may thus modify the *whole-body* geometry. Anticipatory postural adjustments (APAs) are unconscious muscular activities preceding the voluntary movement aiming to prevent the changes in posture produced by the focal movement itself.

The role of APAs in maintenance of the *whole-body* equilibrium has been extensively investigated. Babinsky already observed (Babinski 1899) that in a standing subject, trunk extension is preceded by hip and knee movements in the opposite direction. More recently, it has been also shown that in a standing subject before arm rising, the upper trunk bends backwards (Martin 1967) and a modulation of the EMG activity occurs in leg muscles (Belen’kii et al. 1967). From the sixties a large amount of literature has been mainly devoted to “inter-limb” APAs (see Cordo and Gurfinkel 2004). Conversely, the effects of focal movements on the *segmental* posture have been less investigated. Few examples concern movement of one arm and the related postural fixation in the contralateral side (see Hugon et al. 1982; Baldissera et al. 2008) or “intra-limb” APAs developing in the ipsilateral arm prior to arm (Zattara and Bouisset 1988) or hand movements (Chabran et al. 2001). It should be also underlined that both

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inter-limb and intra-limb APAs precedes fast (Cordo and Nashner 1982) and large movements (Aruin and Shiratori 2004), usually involving large mass segments, i.e. one or both arms, the trunk or the whole lower limb.

However, given that every movement should produce interaction torques on the supporting segments, we were interested in answering the following major questions: (1) are interaction torques engendered by a gentle flexion of the index finger able to perturb the whole arm posture? (2) are interaction torques engendered by a gentle flexion of the index finger effectively compensated by an appropriate chain of APAs? (3) do these interaction torques affect the precision, i.e. the final position, of the intentional movement?

We positively answered the first question by simulating a finger flexion in a four joint arm model and also by measuring, in a real arm, the reactive displacements ensuing to an electrically induced passive index finger tap. Subsequently, we observed that the postural changes predicted by the mechanical model and found in the *in vivo* situation, were, as expected, effectively minimised by APAs on the proximal joints. Lastly, we used the mechanical model to prove that interaction torques produced by finger movement may effectively change the final fingertip position. Accordingly, we propose that a disruption in the APA control may cause a dysmetric movement.

## Materials and methods

Experiments, carried out in five male and five female adult volunteers, were approved by the Ethical Committee of the University of Milano, School of Medicine, in accordance with the standards laid down in the 1964 Declaration of Helsinki. All subjects gave a written consent to the procedure. Their mean ( $\pm$ SD) anthropometric characteristics were: age  $29.4 \pm 9.4$  years, weight  $64.8 \pm 14.2$  kg, height  $169 \pm 10$  cm, index finger length  $9.2 \pm 0.7$  cm, and arm length  $76.9 \pm 7.1$  cm.

### Experimental procedure

The subject was sitting in a chair with his dominant arm lying along the body, the elbow flexed at  $90^\circ$  (either suspended or supported by an armrest) and the hand (prone or supine) in axis with the forearm. With the prone hand, the wrist, finger 1 and fingers 3–5 were lying on a supporting frame, while the index finger was kept extended so that the metacarpo-phalangeal (MP) joint angle was about  $180^\circ$  (see Fig. 2). With the supine hand, the dorsal aspect of the hand was instead lying on the supporting frame, with all fingers relaxed. Subjects were explicitly asked to keep their back supported, the upper-limb still and both feet on the ground

throughout the experiment. The chair was height adjustable and the supporting frame screwed on an articulated arm (Manfrotto 143 MAGIC ARM<sup>®</sup> + 035 Superclamp Kit<sup>®</sup>) so that they were both adapted to the different body dimensions of the subjects. The subject position was always visually controlled by the experimenter.

Subjects were asked to flex their index finger at the MP so as to gently tap and rest on a flat surface. Each movement was self-paced and performed after an acoustic signal delivered by the experimenter. The time between the beep and the movement onset varied according to the subject will. This procedure was adopted to exclude any reaction time.

In each experiment, finger flexion was performed 75 times and EMG from one single postural muscle, together with that from the prime mover FDS was recorded. The 75 trials were accomplished in a temporal window of about 10 min, then the subject had time to rest (about 10 min) before undergoing a new experiment. Subjects never complained about fatigue. Index finger flexion was performed with different hand postures (prone or supine). To avoid an order effect, the different conditions were randomly presented to the subject.

### Movement and EMG recordings

The onset and the end of the fingertip movement were monitored by a pair of capacitive switches (Pepperl and Fuchs, CJ10-30GK-E2). The distance between these two probes was set to 3–4 cm, according to the subject comfort. In some experiments, the index finger movement (flexion–extension on the vertical plane) was measured by a strain-gauge goniometer (Biometrics Ltd, F35) placed across the MP joint. Wrist flexion–extension, on the vertical plane, was instead detected by securing a second strain-gauge goniometer (Biometrics Ltd, SG110) on the dorsal aspect of the hand. Flexion–extension of the elbow was recorded by fixing another SG110 goniometer laterally to the elbow joint. Angular displacements were DC amplified, A/D converted (2KHz) and stored. Goniometer calibration was undertaken before each experimental session.

In each experiment, conventional surface bipolar electrodes (0.8 mm diameter, 20 mm apart) were used to record the EMG signal from the prime mover Flexor Digitorum Superficialis (FDS) and from one of the following muscles: Flexor Carpi Radialis (FCR), Extensor Carpi Radialis (ECR), Biceps Brachii (BB), Triceps Brachii (TB), Anterior Deltoides (AD) and Superior Trapezius (ST). A good selectivity of the EMG recordings was achieved both by a careful positioning of the electrodes and by checking that activity from the recorded muscle, during its phasic contraction, was not contaminated by signal from other sources. However, despite this

care, FCR recordings always contained some FDS activity, due to the strict anatomical proximity between the muscles. On the contrary, FDS activity was selectively recorded by positioning the electrodes on its course in the distal third of the forearm. To probe both excitatory and inhibitory APAs, the subject was requested to maintain a constant level of EMG activation in the investigated muscle (5–10% of that recorded during maximal tonic voluntary contraction during 5 s). The EMG was AC amplified (2–10 k) and band-pass filtered (30–1,000 Hz, to minimise both movement artefacts and high frequency noise), A/D converted (2 KHz), visualised and stored for further analysis.

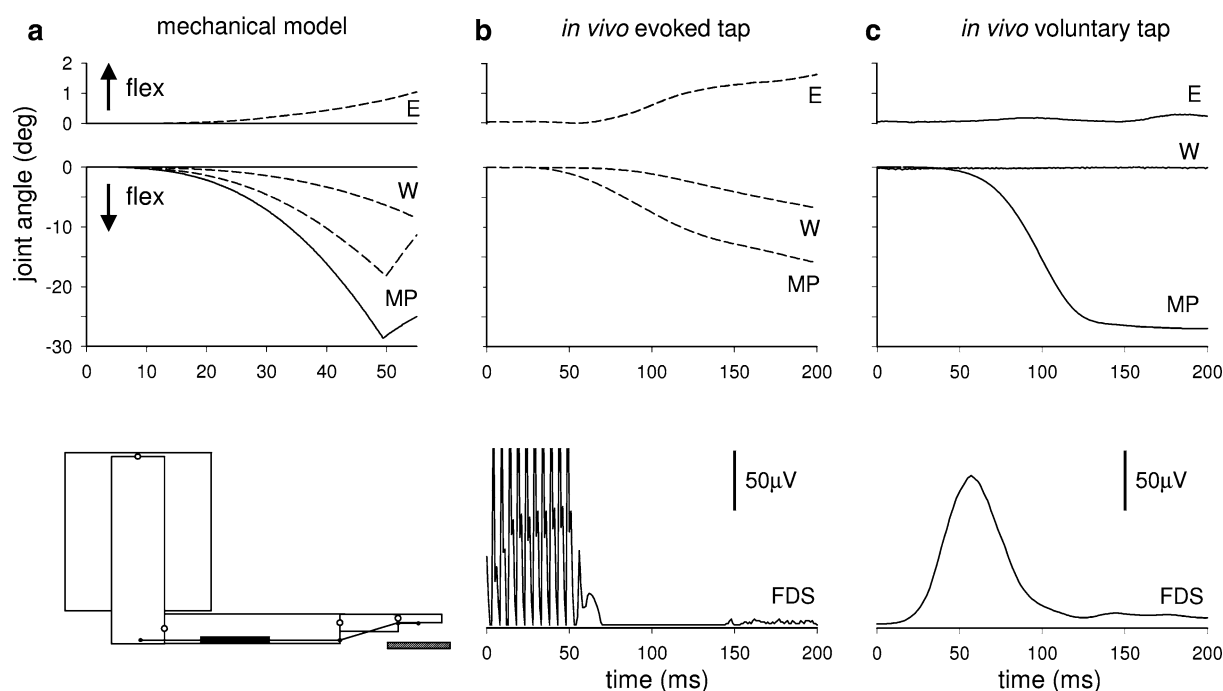
### Mechanical modelling of the finger tap

By using Working-Model2D software, a fictive upper-limb was assembled (see Fig. 1a): all segments were represented by rectangles with size, mass, position of the centre of mass and moment of inertia derived from classical anthropometric tables (Dempster 1955), implemented with data from the NASA-STD-3000 manual (<http://msis.jsc.nasa.gov/sections/section03.htm>). MP, wrist, elbow and shoulder joint were simulated by pin joints with a single degree of freedom in rotation and no translation, i.e. they allowed

only flexion–extension movements in a vertical plane. FDS muscle was reduced to an actuator linked to the distal end of the arm and, via a rope, to the palmar aspect of the index finger. The rope, i.e. the virtual distal tendon, was taut on two pulleys mimicking the palmar ligaments of the wrist and the MP joint. The force exerted by the actuator was chosen so that the simulated finger tapped on a flat surface, placed 3.5 cm from its starting position, after 50 ms. The software allowed measuring the angular rotation of the four joints following the activation of the actuator.

### Passive index finger tapping in vivo

Data derived from the software model were compared to those obtained in vivo after an electrically induced index finger flexion, without any voluntary activity. In this last case, FDS contraction was elicited by transcutaneous electrical stimulation of the median nerve along its course in the forearm, either with single shocks (0.8 ms squared pulses) or with short trains (50 ms duration, pulse interval 5 ms, see Fig. 1b). Site and intensity of the stimulation were set to obtain a passive index finger flexion with a stroke similar to the voluntary one and with a minimal flexion of the other fingers.



**Fig. 1** Angular displacements at metacarpophalangeal, wrist and elbow joints during simulated, evoked and voluntary index finger tap. Time course of a simulated finger flexion at the MP joint and the related changes at wrist (W) and elbow (E) level, all in degree of angular rotation, measured when segments were free to rotate (a, dashed lines) or immobilised (a, fictive APA, solid lines). The modelled arm is sketched in the bottom left inset. Angular

displacements of the three joints were also recorded when an index finger tap was passively evoked in vivo by the median nerve electrical stimulation (b) and when it was voluntary performed (c). Rectified FDS activity in the two lower graphs. Note that the mechanical model well predicts the displacements of the proximal joints both during passive (solid lines) and during voluntary (dashed lines) index finger tap

## Data analysis

In each experiment, the 75 EMG traces of the prime mover and those simultaneously recorded from the postural muscle were digitally rectified and integrated (25 ms). In each prime mover trace, the EMG onset (0 ms in all graphs) was detected by a software threshold (set at 2 standard deviation of the baseline signal) and visually validated. Traces collected from each of the two recorded muscles were then averaged in a fixed temporal window (−1,000 to +300 ms from the prime mover onset). The period of 1,000 ms before the acoustic signal was utilised to calculate a mean reference level for each EMG. In all graphs, the amplitude of the EMG will be expressed in percentage of this mean value. In each experiment, latency of the postural muscle activity, and its amplitude at time zero, were measured off-line on the averaged trace. The onset of an effect in the postural muscle was identified by a cumulative sum technique, coupled to the Monte Carlo method (see Lourenço et al. 2007) and its latency measured from the prime mover onset. Anticipatory activity was thus identified by a negative value.

Since activity in each postural muscles was repeatedly tested in the same subject (2–7 times in different days), for each postural muscle an intra-subject mean latency and an intra-subject mean amplitude were calculated. The intra-subject mean values were then used to compute, for each postural muscle, both the population mean latency and amplitude ( $\pm$ SEM, standard error of the mean, see Table 1). One-sample *t* tests were carried out on the population data to verify, for each postural muscle, that APA latency and amplitude were significantly different from 0. A two-way ANOVA with repeated measures, two hand postures (prone or supine)  $\times$  four synergistic muscles (FCR, BB, AD and ST), was performed on the population

data of APA latency. This aimed both to analyse the single effects of the variables (posture and muscles) and their interaction. Values of *F* and the related *P* will be indicated. For all tests, statistical significance was set at *P* < 0.05.

## Results

Since every voluntary movement is accompanied by interaction torques on neighbouring segments, we were interested in knowing if and how an effortless index finger tap would influence the whole upper-limb posture. A way to face this question was to observe the behaviour of a simple upper-limb mechanical model, in which only the prime mover was represented (Fig. 1a). The model was fed with two parameters obtained during a real voluntary index finger tap (Fig. 1c): a fingertip displacement of about 3.5 cm, and a movement duration of about 50 ms. In this fictive arm, a clear disturbance of both the focal movement, which was reduced in amplitude, and of the upper-limb posture was observed. From the solid line graphs in Fig. 1a, c, it is apparent that the modelled index finger flexion is clearly reduced in amplitude with respect to the in vivo situation (about 19° vs. 25°) and it is also paralleled by relevant changes at wrist (about 7° of flexion) and elbow level (the forearm was slightly flexed, rotating opposite to the wrist). In the model, the only way to prevent these “collateral effects” was to block all segments but the finger, preventing the proximal joints from rotating (fictive APA). If this new condition is modelled, a 28° flexion of the MP joint which produces a fingertip displacement of 3.5 cm, is successfully observed (Fig. 1a, dashed lines). Being aware that this observation derives from a very simplified system, which did not consider either gravity or, for example, the visco-elastic properties of the tissues, we

**Table 1** Mean latency and amplitude of APAs developing in proximal muscles prior to an index finger tap

	APA onset (ms from FDS onset)		APA amplitude (% of reference EMG)	
	Prone	Supine	Prone	Supine
FCR	−74 $\pm$ 11*	−81 $\pm$ 11*	−56 $\pm$ 15*	−23 $\pm$ 6*
ECR	−14 $\pm$ 4	−26 $\pm$ 4	–	–
BB	−65 $\pm$ 8*	−64 $\pm$ 18*	−32 $\pm$ 3*	+39 $\pm$ 12*
TB	−38 $\pm$ 7*	−64 $\pm$ 13*	+22 $\pm$ 7*	−30 $\pm$ 3*
AD	−68 $\pm$ 12*	−95 $\pm$ 12*	−24 $\pm$ 2*	+47 $\pm$ 17*
ST	−90 $\pm$ 14*	−78 $\pm$ 15*	−38 $\pm$ 5*	+37 $\pm$ 9*

Population data from ten subjects (mean  $\pm$  SEM). Data from all muscles but ST were obtained in the supported condition, i.e. with the forearm supported by an armrest. Data from ST were obtained in the unsupported condition, since no APA can be observed in the ST when the forearm is supported. Negative values decreased EMG activity; positive values increased activity. APA amplitude is measured at the onset of the prime mover. Since anticipatory postural effect in the ECR was present in only two out of ten subjects (see text), amplitude of this effect is not included in the table. In each muscle, except ECR, APA onset and amplitude were significantly different from the FDS onset and the reference EMG amplitude, respectively

\* *P* < 0.001, one-sample *t* test

looked also for a more realistic model. To do so, subjects were asked to keep their upper-limb muscles fully relaxed, while finger tap was passively evoked by an electrical stimulation of the median nerve. With such an arrangement, two goniometers placed across the wrist and the elbow were able to detect passive displacements (Fig. 1b) comparable in sign and size to those described by the software model. However, as shown in Fig. 1c, it is apparent that during voluntary finger tapping the MP joint rotation is accompanied by negligible changes in both wrist and elbow position, indicating that the voluntary command should be coupled to a control on postural muscles, intended to minimise the interaction torques arising from the focal movement.

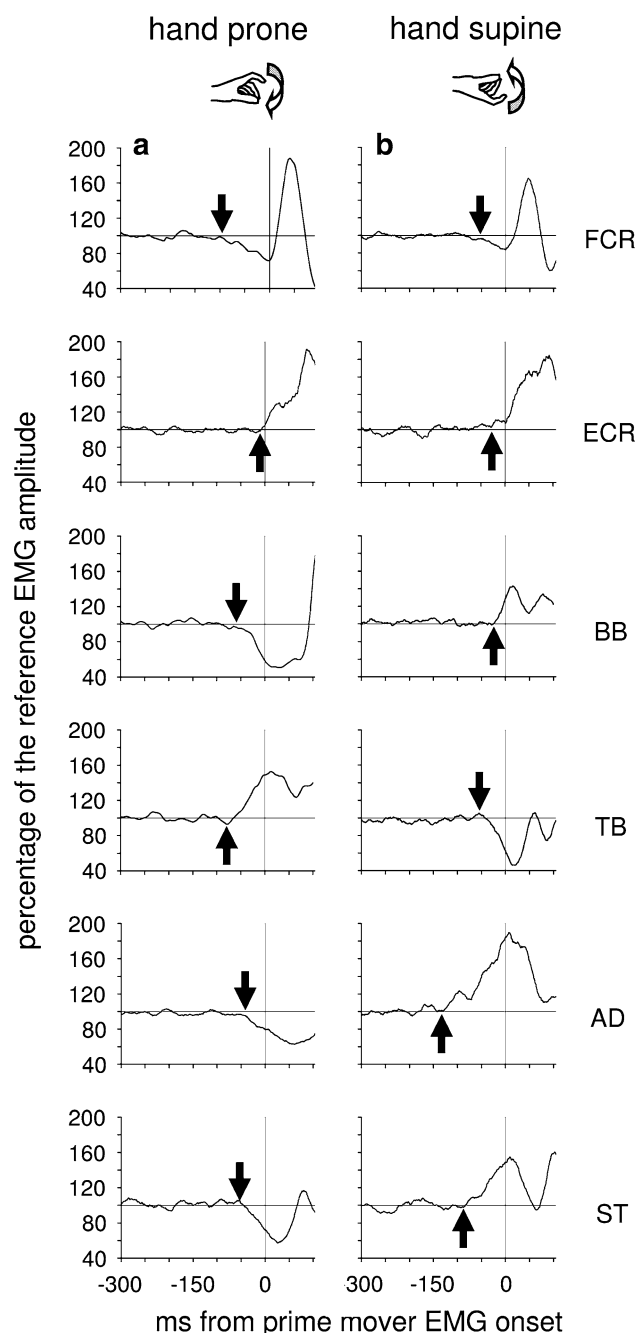
APA prior to index finger flexion with the hand prone

Figure 2 shows the pattern of anticipatory adjustments, observed in a representative subject, when an index finger tap is performed with the prone hand (panel a) or supine hand (panel b).

With the hand prone and supported, FCR tonic activity was regularly reduced before the onset of the FDS burst (vertical line, first row). It is apparent that this EMG reduction is intended to prevent wrist flexion and thus its contribution to the fingertip displacement. Table 1 summarises the population data concerning the APAs onset, as well as their amplitude. An anticipatory increased activity in the antagonistic ECR muscle was present only in two subjects; in eight of them, instead, a clear EMG burst almost paralleled the FDS onset (about 18 ms in the case illustrated in the second row). Due to its timing, the earliest part of this facilitatory activity should be ascribed to a genuine postural feed-forward command, which compensate for the FDS flexing force, acting on the wrist and predicted by the model.

Flexor Digitorum Superficialis activation was constantly preceded also by APAs at the elbow level; a clear inhibition of BB EMG was mirrored by a facilitation of TB (third and forth row). These two effects were similar both for timing and amplitude. Such a reciprocal modulation is the most suitable to minimise the elbow joint flexion (cfr the mechanograms in Fig. 1).

An important anticipatory modulation in the EMG activity could also be observed in the more proximal muscles; when tapping with the prone hand, supported by an armrest, AD activity was always reduced (fifth row), while no effect was detected in ST (not illustrated). Absence of APA in ST suggests that, when the forearm is supported, perturbations of posture evoked by finger flexion are negligible at the shoulder level, so no additional APAs are needed to stabilise this joint during the motor task. However, previous works (see Sect. “Discussion”) suggest that



**Fig. 2** Postural adjustments in upper-limb muscles preceding an index finger tap with the prone or supine hand. Each graph displays the APA onset (arrow) and its development on the tonic EMG from different postural muscles, of a single representative subject, with the hand resting prone (a) or supine (b). The vertical line at 0 ms marks the onset of the prime mover activity. Note that in the muscles acting at the elbow, the shoulder and the trunk APAs reverts in sign when hand posture changes from prone to supine. EMG is rectified, integrated and averaged (75 trials) and its size expressed in percentage of the mean EMG level recorded 1 s before the go signal

the APA chain can be lengthened to muscles far from the moving segment simply by reducing the number of fixation points. Accordingly, when tapping with the forearm



unsupported, a consistent anticipatory inhibition developed also in the ST EMG (last row). This global inhibitory effect would counteract the arm flexion and the scapular elevation which develops when the index finger is flexed and the full APA chain stabilises the more distal joints.

#### APA prior to index finger flexion with the hand supine

Irrespective of the hand posture, prone or supine, FCR activity was always reduced, and ECR increased, prior to FDS activation (cf. Fig. 2a, b). In fact, when passing from prone hand to supine hand, index finger flexion still produce a passive mechanical flexion at the wrist joint. Thus, also in the new postural set these APAs would prevent wrist flexion. Conversely, with the supine hand, BB was regularly excited and TB inhibited (third and fourth rows). This combined reciprocal action, opposite to that observed with the prone hand, counteracts the passive extension of the elbow predicted by the model. This has also been confirmed by analysing this new postural situation with both the mechanical and the in vivo model. Focusing to the more proximal joint the AD muscle, as well as ST, was always recruited in advance to FDS, to counteract the arm extension and stabilise the shoulder.

The two-way ANOVA test aiming to analyse both differences in the single effects of the two variables (posture and muscles) and their interaction, led to negative results (posture,  $F_{1,9} = 0.27$ ;  $P = 0.61$ ; muscles,  $F_{3,27} = 0.85$ ;  $P = 0.47$ ; interaction  $F_{3,27} = 0.08$ ;  $P = 0.47$ ). So, the statistical test did not brought to light any difference in the time distribution of the anticipatory effects in the different muscles or in the two postural sets.

## Discussion

This is the first demonstration that large postural adjustments characterised by an important anticipation from the prime mover may be evoked by a gentle flexion of one single finger. These “intra-limb” anticipatory adjustments show striking similarities to the classical “inter-limb” APAs (see Cordo and Nashner 1982). First, they distributed to several upper-limb muscles and created a postural chain preventing the effects of the interaction torques generated by the focal movement (see Massion 1992).

Second, they reverted in sign when hand posture was changed from prone to supine, i.e. when the direction of the focal movement was inverted (Aruin and Latash 1995). However, a special comment deserves the posture-independent anticipatory action observed in FCR (EMG reduction) and ECR (EMG increase). In fact, due to its trans-wrist course, FDS muscle acts as a wrist flexor both with the prone or the supine hand, thus its mechanical

action, and the associated interaction torques on the wrist do not change with hand posture.

Third, they changed in amplitude according to the level of postural stability (Nardone and Schieppati 1988; Aruin et al. 1998; Slijper and Latash 2000). For instance, Slijper and Latash (2000) have shown that APAs in the ankle muscles are almost suppressed when fast arm movements are performed with an additional finger or hand fixation point. The present work thus confirms that adding an extra fixation point has a dramatic effect on the length of the APA chain, in fact APAs were present in the unsupported forearm while they disappeared when it was leaning on the armrest. However, it should be underlined that in this last situation APAs might still be coupled to voluntary movement, but under threshold for their effect. This argument is postulated by taking into account that when the ipsilateral foot is voluntarily oscillated excitability of the hand motor cortex has been shown to fluctuate under threshold for the motoneuronal firing (Baldissera et al. 2002) and that during a suitable postural condition this “hidden effect” develops in an overt APA (Baldissera and Esposti 2005).

Forth, we are aware that when moving one single finger, the focal movement engenders actions on the neighbouring one (*enslaving* phenomenon, Zatsiorsky et al. 2000). Thus, *parasite* interaction torques may add to those produced by the index finger itself. However, several works have reported a rather independent action of the index finger across a variety of movements (Häger-Ross and Schieber 2000; Reilly and Hammond 2000). Moreover, it has been repeatedly observed that flexion of the index finger is associated with a minimal amount of *enslaving*, largely limited to the middle finger (Zatsiorsky et al. 2000; Lang and Schieber 2004; Kim et al. 2008). For these reasons, it may be assumed that *enslaving* of the neighbouring fingers to flexion of the second one minimally contributes to the anticipatory responses described here and in any case these unavoidable synergies add on, and contribute, to the final response described on the more proximal muscles. This is true for both the results obtained with the prone and the supine hand. In fact, the *parasite* interaction torques in the two postures have the same sign and direction of the reaction to the primary movement.

In conclusion, according to these considerations and on the basis of the most common definition of equilibrium (i.e. a condition in which all acting influences are cancelled by others, resulting in a stable, balanced, or unchanging system) the natural anticipatory synergies coupled to gentle finger tap should be considered as genuine APAs.

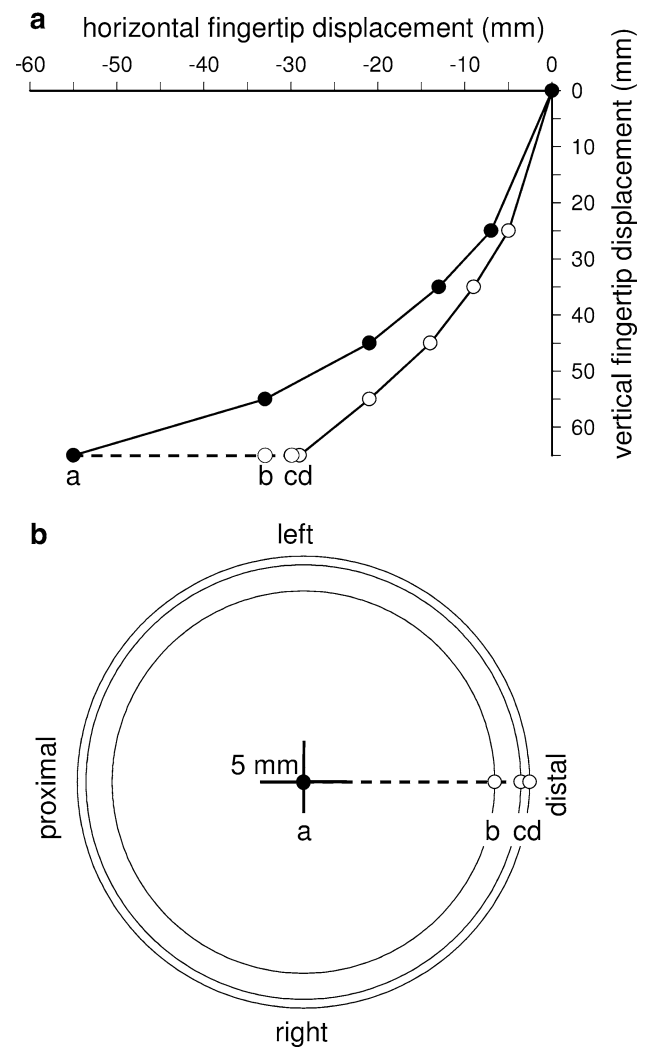
#### APA and dysmetria

Although very simple and fed with basic parameters, the 2D upper-limb model well simulated, in quality and size,

the changes occurring at MP joint when index finger flexion was produced in vivo either by the voluntary activation of FDS or by its passive electrical recruitment. This model was also useful to predict the effects exerted on the more proximal joints (wrist and elbow) by the interaction torques generated by the focal movement. The model has also made apparent an aspect of motor control which may be related to APAs; in fact, the anticipatory adjustments not only would guarantee both a fixation chain for the prime mover and the maintenance of the whole-body equilibrium, but could be also very important in controlling the trajectory and the final position of a moving segment.

Actually, the model simulation shows that when proximal segments are immobilised (filled circles in Fig. 3a and continuous lines in Fig. 1a), the finger hits the horizontal plane always more proximally than when joints are left free to rotate (white dots). From the simulation, a change of 4 mm in the final position is expected when the vertical displacement is 35 mm, i.e. the current stroke used during finger taps. Moreover, the horizontal displacement is exponentially growing with the movement amplitude, reaching 26 mm for a stroke of 65 mm. From Fig. 3 it is also evident that immobilisation of the shoulder and the elbow minimally affects the final fingertip position as compared to that obtained by blocking the wrist joint; for a vertical displacement of 65 mm, a block acting on the shoulder shifts the hitting point of only 1 mm (compare circles d and c, in Fig. 3a), a block on both shoulder and elbow moves it of 4 mm (d vs. b) while immobilising also the wrist changes the final position of 26 mm (d vs. a). Thus, it is easy to predict that any disturbance in the APA control would set the hitting point along the line drawn between the two limit situations. If the same horizontal fingertip displacements are now plotted in a planar graph (Fig. 3b), in which also lateral displacements of the index finger are considered, a final fingertip position would be represented by one single point of the plane; for example with a full APAs control, the target position would necessarily be the black point with coordinates 0:0. Instead, a disturbance in distribution, amplitude and/or timing of the APA chain would result in an impact of the finger in another point of the plane, in other words an altered APA would end in a dysmetric index finger movement.

Since it has been shown that patients with focal or diffuse lesions of the cerebellum couple to the focal movement APAs which are abnormal in latency, duration and amplitude (Diener et al. 1990; Diedrichsen et al. 2005), we propose that dysmetria could also be the expression of an APA disturbance. Broadening the classical view, dysmetria may not only due to an altered activation in time and amplitude of the prime mover and its antagonist muscle (Vilis and Hore 1977), but also by an impairment in compensating the interaction torques, as previewed by



**Fig. 3** APA and dysmetria. Model simulation of the horizontal fingertip displacement, as function of different strokes, when the proximal segments are immobilised (**a**, fictive APAs, filled circle), and when they are free to rotate (**a**, empty circle). Note that for a vertical displacement of 65 mm, the fingertip hits the table surface (dashed line) more proximally with APAs (**a**) than when no-APAs are involved (**d**). Dots **b** and **c** mark the hitting position when the APAs concern the sole shoulder or shoulder plus elbow, respectively. In the planar graph (**b**), in which also lateral segment displacements are considered, the filled circle is the univocal target position resulting from a fully correct APA control, a disturbance of the APAs chain would necessarily produce the impact of the fingertip in any other point

Topka et al. (1998). We are aware that the role of the cerebellum in the genesis or in the transmission of the APAs still remains open; however, it cannot be excluded that a “timing machine”, as the cerebellum is, parallelly contributes to the control of the focal movement and its parallel natural synergies.

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